

AMAZONIANA	VI	4	537 – 555	Kiel, Januar 1979
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## The Evolution of the *Liolaemus Wiegmanni*-Complex and the Dispersal Centers in Brazil.

by

Paul Müller

University of Saarbrücken, Germany

Every organism, population and living system contains informations, the clarification of which supplies criteria for a genetic and/or ecological evaluation of landscapes. Morphological, ecophysiological or ethological similarities between phylogenetically different groups can promote the understanding of identical or similar challenges, to which an organism or a population in a certain location is exposed. Similar life forms among organisms, the comparable diversity of ecosystems, as well as the structures of populations and biocoenoses can be utilized to elucidate the ecological affinity of different regions. However, these factors alone do not suffice as "affinity-criteria"; indeed they can lead to grave misinterpretations if the connections between form and function are not adequately understood.

If we use organisms, biocoenoses and ecosystems as indicators for environmental quality and the typification of relationships between regions, then both their ecological and genetic structures have to be given equal consideration. This prerequisites that only time periods be analyzed, in which a definable, characteristic constancy of a taxon's ecological valence can be assumed.

Numerous examples show that basic phylogenetic innovations generally accompany an incisive change in environments and therefore also a change in the ecological valence of populations or parts of populations. In the case of vertebrates (especially the poikilothermic reptiles and the homeothermic birds), allopatrically distributed sub- or semi-species within one species or closely-related group of species belong to the same or similar biomes in most instances (KEAST 1961, MOREAU 1966, MÜLLER 1973, 1977), whereas on their genus and family levels ecological pluripotency is often the case. Since "being similar" does not necessarily mean "being related", in general only groups with the most complicated structures and numerous characteristics are suited for clarifying and phylogenetically reconstructing the relationships between higher taxons, in order to distinguish between synapomorphies and convergences (HENNIG 1969, ILLIES 1965, BRUNDIN 1972, SCHMINCKE 1974, ZWICK 1974).



An analogous situation presents itself with respect to ranges. Whereas for example a monotypic genus can be used to reconstruct the phylogenesis (i.e. the sequence in the development of features and therefore of taxa), the geographical origin of the perhaps completely isolated range of this genus can neither be solely explained by chorological nor phylogenetic means. The length of time a species has lived in a certain terrestrial location rarely coincides with the geological age of that location. The assumption that a taxon's present range — regardless of the existence of apomorphic or plesiomorphic features — possesses structures homotopic to its center of origin or to one of the many dispersal centers which are possible in the course of its evolution, has yet to be established in the individual case through careful structural analysis.

### 1. The Analysis of Dispersal Centers as a Criterion for the Affinity of Regions

If we try to explain the affinities of Brazilian animal species and communities, we have to utilize methods, whose results establish the evolutionary history and ecological affinity of landscapes through knowledge about the evolution and present-day ecology of taxa. The explanation and chorological definition of dispersal centers represent one possible approach. At this point it seems important to me to discuss in detail the problems which accompany the analysis of dispersal centers. For the results of such an analysis contribute to a better understanding of the recent evolutionary history of organisms and to the clarification of historical facts concerning the earth and climate and therefore to a deeper awareness of the landscape's present status. Thus dispersal centers are just as important for evolutionary research as for the field of geography.

Dispersal centers are regions in which populations survived in spite of unfavorable environmental circumstances. Naturally a region can only then function as a dispersal center, if its environmental conditions as a whole do not cause the extinction of the biocoenoses living within it. In addition, as long as the unfavorable conditions prevail, the populations in a dispersal center are isolated from other regions and populations.

This enables geographical isolation (separation), an important force affecting the development of species and races, to work. In order to avoid misinterpretations, it should be pointed out, however, that dispersal centers do not necessarily represent centers of origin (MÜLLER 1973, 1977). In order to resolve this question, one has to investigate whether the areas of distribution are situated close to species's area of origin (= plesiochoric) or whether they have moved away from the center of origin in the course of a species' evolution (= apochoric; compare MÜLLER 1972, 1977).

Prerequisite to clarifying these points for higher taxa (genera, families), is a thorough description of their evolutionary history, which has only been completed for a few animal groups, however. For this reason it seems sensible to limit the analysis of dispersal centers to the consideration of species, super-species and subspecies for the time being. For a sub- or semi-species it is easier to prove the apo- or plesiochory of its range with respect to its last functional dispersal center (allopatric distribution, etc.) than for a species. However, it should be emphasized that the development of races is not necessarily due to geographical isolation of originally homogeneous populations (MÜLLER 1977).

The interrelations of the refugial phases of ranges, the dynamics of ranges, migrations and differentiation give reason for distinguishing between three types of subspeciation: a) refugial subspeciation; b) extrarefugial subspeciation; and c) peripheral subspeciation.

Peripheral subspeciation can take place through fluctuation in the boundaries of a range, but also through suppression, according to REINIG (1970); by this term he means the repression of phylogenetically older — by younger subspecies with dominant alleles, in which case selection does not play a part. Thereafter, phylogenetically older, peripheral races would be the remaining populations of subspecies that were originally more widely distributed and overrun in the center of their range by younger subspecies. These older types do not have to accumulate exclusively on the geographical limits of the range, but can also be preserved near ecological boundaries (e.g. mountains) within the area of distribution.

These qualifying statements are a necessary prerequisite to a correct evaluation of dispersal centers. The analysis of dispersal centers presupposes three steps. First the minimum ranges of species, semispecies and subspecies are projected on the map of a continent or an animal kingdom. Only in rare cases do individual ranges possess common areas on the periphery, however always in the nuclear area where they overlap. That the distributional centers obtained in this way are not necessarily centers of origin, was numerous studies. These centers are regions with maximum range diversity. At this stage of the analysis, they can evidence either ecological or historical causes, or both. Whether they are dispersal centers, that is preservation centers of fauna and flora during the prevalence of unfavorable environmental conditions, can first be ascertained through a further examination of the relationships between the fauna which belong to the different centers. Therefore in the second step of the analysis, polycentric ranges (large ranges with several nuclear areas) of polytypic species must be superimposed on the same region. This projection often, but not always results in the discovery that different small-range species' - and subspecies' distributional centers (or semispecies' distributional centers) coincide. In a third step, which is usually forgotten in zoogeographical work, the formation of subspecifically or semispecifically differentiated vicariants has to be clarified (MÜLLER 1972, 1973, 1977). The classification of a differentiated population under a certain type of differentiation can generally be justified, if hybrid belts exist where the originally separated populations came into contact.

In the field, however, it is usually difficult to recognize hybrid belts, as not every population with intermediary characteristics has to be a hybrid population. If it can be shown, that a dispersal center is based on patterns of differentiation which can only be interpreted as products of geographical isolation, and that the populations can be considered plesiochoric, then one can assume that dispersal centers, as homotopic structures, underlie distribution centers.

Dispersal centers did not only develop during the Pleistocene by any means, although this is often maintained. Refuges can develop at any time, even in the present and can function as dispersal centers when the unfavorable phase is over.

Every species has at least one dispersal center that coincides with its center of origin. During the course of their development however, the regions can become widely separated from one another. The established dispersal centers, therefore, simply represent areas in



which populations ultimately survived the unfavorable environmental conditions affecting them.

## 2. The Dispersal Centers of South and Central Brazil

An analysis of the dispersal centers of terrestrial vertebrates in the Neotropical realm (details in MÜLLER 1973) revealed that at least 40 centers exist. A study of the relationships between the individual centers, based on the phylogeny of their faunal elements (on the semi- and subspecific levels) resulted in the classification of the centers into three main groups. The faunal elements of Group I (non-forest) are characterized by their adaptation to unforested or at least partially-unforested biomes, generally below 1.500 m. The faunal elements do not occur in the rain forest biomes, which are inhabited by the elements of Group II (forest and montane forest), while those of Group III show an ecologically restrict adaptation to the treeless high-mountain region (oreal). Within these three main groups, the individual centers can be further categorized into subgroups representing even closer affinity (the montane forest centers, etc.) or into sets with relationships to other groups or centers outside the Neotropical region.

In Central and Southern Brazil the following centers exist:

### 2.1 The Para Centre

The Centre is limited in the west and north by the Rio Tocantins, and by the northern part of the Rio Araguaia south to Matheus; in the south it is limited by the Serra do Gurupi of the northern part of Maranhão and by the Rio Grajau, through some species extend as far as the Rio Paraíba. The rain forest of the island of Marajó, which lies just north, has only a slight connection with the Para Centre in its fauna. Some typical Para elements are represented both in the Para Centre and on Marajó i.e. *Aulura anomala*, *Iphisa elegans*, *Leimadophis oligolepis* and *Amphisbaena mitchelli*. The other species which occur in both, however, have very widespread and sometimes strongly disjunct distributions. The Para faunal elements *Pipa snethlagae*, *Eupemphix paraensis* and *Leptodactylus matinezi* have not been found on Marajó.

*Bothrops bilineatus*, which I found on Marajó in 1965, has a very interesting range. It shows connections on the one hand with the Para, Guyanan and Amazon Centers and on the other with the Serra do Mar Centre. At the same time the relationship is much closer between them and the Amazon Centre (*B.b. smaragdinus*). It would be premature to conclude from this, however, that the Para Centre and Serra do Mar Centre are very closely related.

Again there is a herpetological example which is supposed to show the relationship between the forests of the Serra do Mar and the Para Centre but which seems dubious to me. This is the Anguid *Ophiodes striatus* which, as I have been able to show in several places in its south-east Brazilian range, is in no way a rain-forest form. Moreover its occurrence in Para is doubtful. Only *Eleutherodactylus binotatus* can be used to show a relationship between the Serra do Mar and Para Centres.

The numerous species distributed both in the Serra do Mar and Amazon Centres are mostly polycentric and widespread in the Amazon area. In addition there are species with

disjunct ranges which have been found up till now only in the Amazon and Para Centres. This disjunction cannot yet be clearly interpreted, but is found in fishes and reptiles (*Lepidoblepharis festae*).

The position and limits of the Para Centre in the north, east and south can be explained well enough from present-day ecology. Stretches of water, even narrow ones, act as barriers to strict rain-forest species and open landscapes have a similar effect.

### 2.2 The Madeira Centre

This centre is limited in the north by the Amazon, in the west by the Madeira and Beni, in the east by the Xingu and in the south by the Bolivian Eastern Cordillera.

### 2.3 The Caatinga Centre

The position of this centre is defined by the ranges of *Crotalus durissus cascavella*, *Bothrops erythromelas*, *Epicrates cenchria xerophilus*, *Limadophis poecilogyrus xerophilus*, *Tropidurus semitaeniatus* and *Gymnodactylus geckoides geckoides*. The endemism of the Caatinga Centre is greater than that of the Chaco Centre and in reptiles is 10 % of the total. In the Chaco Centre endemic amphibians are almost entirely lacking, but this does not hold to the same extent for the Caatinga Centre.

Thus even within the genus *Physalaemus* there are three species that can be reckoned as Caatinga faunal elements i.e. *Ph. cicada*, *Ph. albifrons* and *Ph. kroyeri*, and there are two such elements in the Leptodactylidae i.e. *Odontophrynus carvalhoi* and *Pleurodema diplostictis*. The closest relatives of the Caatinga faunal elements occur in the Chaco Centre and the Campo Cerrado Centre.

### 2.4 The Campo Cerrado Centre

The faunal elements of the Centre are adapted to the vegetational formation of the Campo Cerrado.

The reptiles and amphibians have a number of remarkable endemics which indicate with certainty the close relationship of the Campo Cerrado Centre with the Chaco and Caatinga Centre. These are:

*Epicrates cenchria crassus*  
*Lygophis lineatus dilepis*  
*Chironius flavolineatus*  
*Bothrops moojeni*  
*Hoplocercus spinosus*  
*Bufo granulosus major*  
*Bufo rufus*  
*Hyla fuscovaria*  
*Eleutherodactylus heterodactylus*  
*Leptodactylus chaquensis*  
*Leptodactylus gualambensis*

*Lygophis paucidens*  
*Crotalus durissus collilineatus*  
*Leimadophis poecilogyrus intermedius*  
*Cnemidophorus ocellifer*  
*Bufo paracnemis*  
*Bufo ocellatus*  
*Hyla raniceps*  
*Ceratophrys goyanus*  
*Leptodactylus breviceps*  
*Leptodactylus pentadactylus labyrinthicus*  
*Hypopachus muelleri*

### 2.5 The Uruguayan Centre

The position of this Centre, can be defined on the ranges of its faunal elements: *Leptodactylus gracilis*, *Physalaemus henseli*, *Anopsibaena kingii*, *Pleurodema darwini* and *Cthonerpeton indistinctum*.

For faunal elements that are not very vagile the Rio Parana forms the western and



southern limit of the Centre while the rain-forest biome of Rio Grande do Sul and Santa Catarina forms the northern limit. A zoogeographical analysis of the herpetofauna of the island of Florianópolis showed that 20 % of the species could be reckoned as Uruguayan faunal elements. This cannot be explained from the present-day ecology since the island is screened off to the south from the Uruguayan Centre by the rain-forest biome of the mainlands.

## 2.6 The Parana Centre

The Centre can be defined on the ranges of *Bothrops cotiara* and *Amphisbaena mer- tensi*. The occurrence of *Araucaria angustifolia* together with the Parana faunal elements indicates only that both prefer to live in this relatively high-lying area above 800 m.

## 2.7 The Serra do Mar Centre

The Centre lies in the rain-forest biomes of the Brazilian coastal range i.e. the Serra do Mar, broadly understood. It extends from the state of Santa Catarina in the south to the state of Pernambuco (and Paraíba) in the north, including the continental islands off-shore to these states. Except for Florianópolis, the islands off the coast within the 50 m isobath have a purely forest fauna.

Analysis of the endemism of the area shows that the Serra do Mar Centre has the highest absolute numbers of monotypic bird and amphibian genera of any centre.

In the amphibian family Hylidae at least 71 species can be reckoned as faunal elements of the Serra do Mar Centre.

On checking localities the Iguanids *Anisolepis grilli*, *Anolis nasofrontalis*, *Enyalius bibroni*, *E. iheringi* and *E. catenatus* are faunal elements of the centre as also are the Teiids *Arthroseps wernerii*, *Anotosaura collaris*, *Colobodactylus taunayi*, *Placosoma cordylinum* and *Stenolepis ridleyi*, which both belong to monotypic genera. The same holds for the Crotalids *Bothrops megaera*, *B. jararaca*, *B. jararacussu*, *B. insularis*, *B. pradoi* and *B. pirajai*. The Serra do Mar Centre can be divided easily into three subcentres. The northernmost lies between Salvador (= Bahia) and Recife and can be called the Pernambuco subcentre. The second subcentre, which is adjacent to the Pernambuco subcentre and south of it, lies in the rain-forest biomes of Ilheus and can be called the Bahia subcentre. The third and most important of the subcentres is the Paulista subcentre (c.f. MÜLLER 1973).

The position of dispersal centres has been decisively influenced by Quaternary oscillations in climate and fluctuations in the vegetation. The dispersal centres and their faunal elements can be used to indicate how the landscape evolved in the area in question. One example is the *Liolaemus wiegmanni* Complex.

## 3. The *Liolaemus wiegmanni* Complex and the History of the Brazilian Restinga

The some 50 species of the South American ground lizards of the genus *Liolaemus* occur from the Andean Puna-Highlands to the moist Nothofagus-Forests of Chile and cold steppes of Patagonia and even in the subtropical and tropical Restinga and coastal dune regions of East Brazil (MÜLLER 1976). Besides euroky species, stenoky species with often very disjunct areas are present.

Especially with this latter group intensive research has been done of late as to phylogeny, ecological habitat bonds and areal history, in an attempt to contribute to the developmental history of South American landscapes. This is also true for Brazilian populations of this genus, which were described as "Restinga- or coastal dune species" (DANSEREAU 1947, GLIESCH 1923, JAKOBI 1977, MERTENS 1938, 1957, MÜLLER 1976, VANZOLINI and AB'SABER 1968).

Two allopatrically distributed species, *L. lutzae* (Restinga of Rio de Janeiro and Guanabara) and *L. occipitalis* (coastal dunes of Parana, Santa Catarina, Rio Grande do Sul and Uruguay) were thought to be "closest relatives" and in an ingenious study, by means of dating the postglacial phases of dune formations, VANZOLINI and AB'SABER (1968) tried to determine when the geographical separation of *occipitalis/lutzae* had taken place and thus *L. lutzae*'s rate of evolution. "Geomorphic data permit dating the spread of the ancestral population and the isolation of peripheral populations at some time between 3.700 and 2.500 B.P.". Although the existence of quaternary and postglacial "coastal migration routes" is documented by many palaeontological, geomorphological, climatological and biogeographical findings, several facts contradict this attempt to date the spread of the original populations of *L. lutzae*:

- a) The island faunas in the state of São Paulo are pure "forest faunas" (MÜLLER 1970).
- b) In the postglacial Restinga- and coastal dune landscapes of São Paulo isolated remaining populations of *Liolaemus* obviously do not exist.
- c) An expansion of the Restinga within the granite- and gneiss-block-zones of the Serra do Mar was impossible during the late postglacial in many places due to the minimal variation in the height of sea level (BIGARELLA 1965, 1971, STEVENSON and CHENG 1969).
- d) The relationships of *L. lutzae* and *L. occipitalis* to other *Liolaemus*-species were not sufficiently taken into consideration up until now.

There are really three species in Brazil which constitute a superspecies-complex (MÜLLER and STEINIGER 1977) with the allopatric semispecies *lutzae*, *occipitalis* and *wiegmannii*. They are not only morphologically and chorologically different, but also prefer different biotopes and show different electrophoretic patterns in their proteins and esterases. The author was able to investigate the distribution and ecology of the *Liolaemus*-species in Brazil on several trips there (1969, 1974, 1976, 1977, 1978) and brought numerous live specimens back to Germany, where they were examined karyologically and electrophoretically etc. in the laboratory.

## 3.1 Methods and Materials

The distribution of the species was determined with a high degree of accuracy by means of systematic investigation of the Restinga- and coastal dune landscapes from the southernmost Rio Grande do Sul to Rio de Janeiro. Nevertheless, due to the size of the research area, a few chorological questions as to the exact northern and southern boundaries of the three species are subject to discussion. In September 1977 all (!) potential biotopes between São Sebastião (state of São Paulo) and Angra dos Reis (south of Rio de Janeiro) were reexamined, but no *Liolaemus*-species could be found. The same is true for the coast of Parana (October 1976); however, JAKOBI (1977 and in litt.; cf. MÜLLER 1976) reported the existence of *Liolaemus* in the dunes near Paranaguá. From the states of Parana and São Paulo document specimens are still missing, but are present from all the localities we discuss here. Autecological and synecological research was done in the terra typica of *L. lutzae* (Recreio dos Bandeirantes, Rio



de Janeiro), at the localities of *L. occipitalis* (Tramandai, Jardim do Eden; Rio Grande do Sul; Florianópolis, Lagoa da Conceição, Santa Catarina) and of *L. wiegmanni* (Tapes, Rio Grande do Sul) in September, October 1974, 1976 and September 1977. For the electrophoretic separation of the serum proteins, *Liolaemus* specimens from the following localities were examined: Torres (4 specimens), Rio Grande (4 sp.), Tramandai (2 sp.), Florianópolis (1 sp.), Laguna (1 sp.), Tapes (5 sp.) and Rio de Janeiro (3 sp.).

The electrophoresis was performed with the disc-electrophoresis-apparatus DEA 90 of the WTW Company in Weilheim. Polyacrylamide was used as a separation medium and was polymerized in glass tubes 140 mm long with an inner diameter of 6 mm. The separation of the proteins and enzymes was done vertically, using the improved (MAURER and ALLEN 1972) discontinuous buffer- and gelsystem of ORNSTEIN (1964) and DAVIS (1964).

The following stock-solutions were prepared, and enough distilled water was added to each, so as to equal 100 ml:

- (1) 36,6 g Tris (hydroxymethyl) aminomethane  
48,0 ml 1 N HCl  
0,23 ml N, N, N', N'-tetramethylethylenediamine
- (2) 28,0 g Acrylamide  
0,735 g N, N'-methylene-bis-acrylamide
- (3) 0,14 g Ammonium persulfate
- (4) 5,98 g Tris (hydroxymethyl) aminomethane  
48,0 ml 1 N HCl  
0,46 ml N, N, N', N'-tetramethylethylenediamine
- (5) 10,0 g Acrylamide  
2,5 g N, N'-methylene-bis-acrylamide
- (6) 4,0 mg Riboflavin
- (7) 40,0 g Sucrose (Saccharose)

For the polymerization of the small-pore separation gel the stock solutions (1), (2), distilled water and (3) were mixed in the (volume) proportion 1 : 2 : 1 : 4. A mixture of the stock solutions (4), (5), (6) and (7) in the ratio of 1 : 2 : 1 : 4 was prepared for the polymerization of the large-pore spacer gel. For the cap gel the same mixture as for the spacer gel was used.

The height of the separation gel in the glass tube was 12 cm and 1 cm for both spacer and cap gels. The electrophoretic separation took about seven hours per tube of gel by a current intensity of 2,5 mA. A Tris-Glycine-Buffer served as electrode buffer (pH 8,3). The separation was performed at room temperature 22 - 23 °C).

In order to obtain the serum samples, the animals to be examined were anaesthetized and decapitated so that aortas and carotids were cut. The mixture of venous and arterial blood which flowed out was absorbed with a round filter paper 5 mm in diameter. According to a modified method of the direct disc-tissue-electrophoresis of MITTELBAACH, ANTLE and HAMBURGER (1969) resp. MITTELBAACH and HAMBURGER (1969) the blood serum-soaked filters were applied directly to the already polymerized spacer gel. To prevent the sample-proteins from mixing with the electrode buffer, cap gel was polymerized over the sample immediately.

Several samples were taken from each specimen, so that the activity of the fernal proteins and esterases could be shown at the same time.

The general proteins were stained with Coomassie Brilliant Blue R-250. Immediately after being removed from the glass tubes, the gels were put into a solution of 0,02 % Coomassie Brilliant Blue R-250, 5 % methanol and 7 % acetic acid (in a proportion of 1 : 1 : 1) and were left standing overnight.

Destaining took place every 8 to 10 hours using a solution of 5 % methanol and 7 % acetic acid. The gels were evaluated visually on a lighted viewing table. For the investigation of the esterase activity the removed gels were placed in a 0,5 M boric acid solution (pH 4,1) for 90 minutes in order to reduce the pH-value of the gel for an optimal esterase reaction. The preincubation in boric acid took place at a temperature of + 4 °C, so as to keep the diffusion of the proteins in the gel at a minimum (SIMS 1965). After this the gel were thoroughly rinsed with distilled water and incubated in a solution of 30 mg -naphthylacetate and 75 mg Fast Red TR-salt in 150 ml of a 0,1 M phosphate buffer solution (pH 6,5) (HUBBY and LEWONTIN 1966). After about two hours the esterase bands had their final colour. They were evaluated using the densitometer DD 2 (KIPP and ZONEN Company).

### 3.2 Relationships of the Brazilian *Liolaemus*-Species

#### 3.2.1 Morphological criteria

Three *Liolaemus*-species, coming from the South, have reached Brazil (cf. Discussion):

*Liolaemus lutzae* MERTENS 1938, *Liolaemus lutzae* MERTENS, Zool. Anz., 123 - 221, fig. 1. Terra typica: Recreio dos Bandeirantes, Rio de Janeiro, Brazil.

*Liolaemus occipitalis* BOULENGER 1885, *Liolaemus occipitalis* BOULENGER, Ann. Mag. Nat. Hist., (5) 15: 192. Terra typica: Rio Grande do Sul, Brazil.

*Liolaemus wiegmanni* (DUMÉRIL and BIBRON) 1837, *Proctotretus wiegmanni* DUMÉRIL and BIBRON, Erp. Gén., 4: 284. Terra typica: Chile (?).

The *L. glieschi* from Torres described by AHL (1925) is rightly considered synonymous with *L. occipitalis* by MERTENS (1938).

Morphologically the three species can easily be distinguished (MERTENS 1938, VANZOLINI and AB'SABER 1968). A few distinguishing characteristics, which were not sufficiently taken into consideration so far, shall be appended here:

*L. lutzae* (52 specimens examined) as well as *wiegmannii* (27 specimens examined) have a contrasting brown stripe on their back, several dorsal scales wide, which extends from the head to the middle of the tail. In addition *wiegmannii* exhibits a thin, light-coloured vertebralline running down the center of this brown stripe. *L. lutzae* has just a hint of this line, but only down the first third of its back. By both species the brown dorsal stripe is bordered by two light para-vertebral bands. The significant difference in colouring between the two species is in the blackish-brown spots with a light border: by *wiegmannii* these run along either side of the light vertebral line like a string of pearls; as to *lutzae*, they are separated by the brown dorsal stripe and are close to the bright para-vertebral lines. *Occipitalis* has no brown dorsal stripe (349 specimens examined) and if spots appear on the grayish-white dorsal scales at all, they are never as prominent as by *lutzae* and *wiegmannii*.

The number of scales around the center of the rump (*occipitalis* = 64 - 76; *lutzae* = 56 - 63; *wiegmannii* = 45 - 54) has also proved a good distinguishing characteristic. On the other hand, spots on the throat that VANZOLINI and AB'SABER (1968) considered an identification criterium for *occipitalis*, can be missing to a great extent by some populations.

The indication that *lutzae* is considerably smaller than *occipitalis* is often found in literature. "*L. occipitalis* is a larger form, specimens 65 mm long (snout to vent) being common; *lutzae* hardly reaches 50 mm" (VANZOLINI and AB'SABER 1968). However, an examination of type and paratype in the Senckenberg Museum revealed that the individuals on which MERTENS' description was based were young ones. Therefore, the information about *lutzae*'s size has to be revised. Two specimens from the Restinga da Tijuca (Rio de Janeiro), being kept alive in Saarbrücken, are at least 72 mm long from head to rump, and therefore even larger than the *occipitalis*-specimens from Rio Grande.

#### 3.2.2 Karyotype

Research performed by ESPINOZA and FORMAS (1976) showed that *Liolaemus pictus* and *L. cyanogaster*, which are sympatrically distributed in Chile and Argentina (Nahuél Huapi), have a 2n = 34 set of chromosomes as the Brazilian *L. lutzae* does.



"... the karyotypes show 6 pairs of macrochromosomes and 11 pairs of microchromosomes, of which the first pair is very large". The *L. lutzae* (Rio de Janeiro), *L. occipitalis* (Rio Grande, Tramandai) and *L. wiegmanni* (Tapes, Rio Grande do Sul) that we examined, have the same set of chromosomes and karyotype. Thus for the first time,  $2n = 34$  is confirmed for *L. occipitalis* and *L. wiegmanni* as well. This set of chromosomes was also found by species of the Iguana-genera *Uma*, *Sceloporus* and *Anolis*. Since it is generally assumed that the evolution of the neotropical Iguanas - similarly to that of the cricetid rodents (cf. GARDNER and PATTON 1976) - can be characterized by a reduction of the chromosome sets ( $2n = 36$  is considered "primitive" for Iguanas), it is probable that the karyotype of *Liolaemus* came about by means of centric fusion. This presumption is supported by the existence of an especially large pair of microchromosomes.

### 3.2.3 Electrophoretic Results

In accordance with the morphological findings, the general protein pattern and esterase-isozyme-pattern of the blood serum confirms that three closely-related species exist. The distributional pattern of the proteins comprises 20 separate bands. These were numbered consecutively according to their rate of migration from the cathode to the anode. A first comparison of the distributional pattern of the protein bands of the specimens from the seven localities (the patterns of individuals from the same biotopes were almost identical) reveals that 11 bands (Nos. 6, 8, 9, 12, 13, 15, 16, 17, 18, 19 and 20) emerge for each of the examined animals (although in varying intensity and with slight differences in migration speed). The bands no. 6, 18 and 20 have almost the same intensity and seem to be genus-specific. But to prove this assumption, an examination of related genera would be necessary.

Within their band-spectrum the animals from Torres, Rio Grande, Tramandai, Florianópolis and Laguna exhibit almost identical bands, which justifies their classification to the species *L. occipitalis*:

The pattern for this species is made up of 10 to 12 bands. With respect to the animal of Florianópolis band no. 19 is missing; band no. 13 of the only examined specimen from Laguna is more intensely coloured.

The distributional pattern of the examined individuals from the population of Tapes (= *L. wiegmanni*) is much more diversified. It shows altogether 18 very distinct protein bands. 11 of them correspond to those of *L. occipitalis* (although band no. 19 is much closer to the cathode) and seven new bands appear.

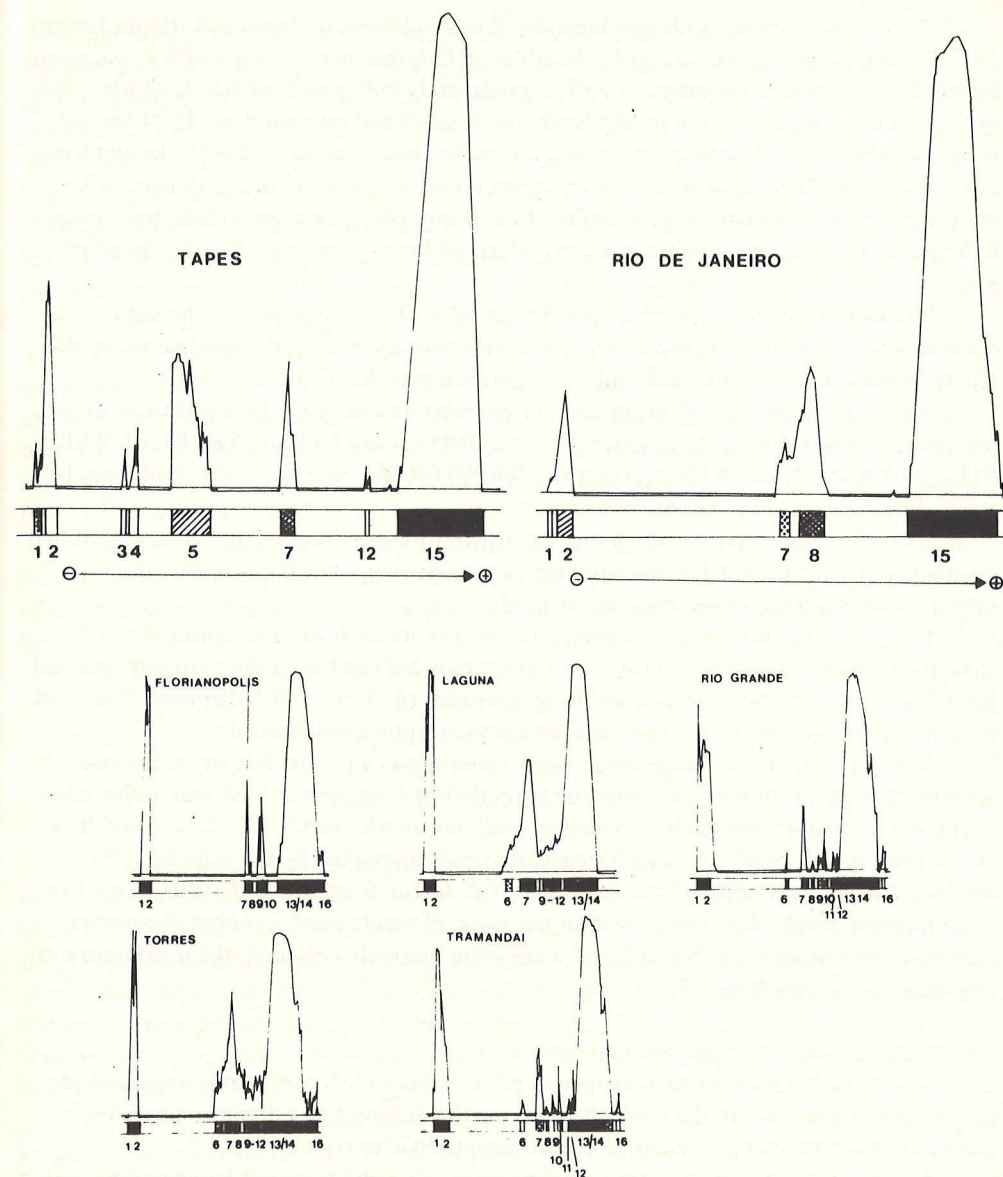


Fig. 1:  
Densitograms of esterase pattern of the *Liolaemus* populations from Tapes and Rio de Janeiro, Florianópolis, Laguna, Rio Grande (City), Torres, and Tramandai.



Two of these seven bands are shared by the populations of Tapes and Rio de Janeiro (= *L. lutzae*), i.e. bands no. 10 and 11. In addition *L. lutzae* has 11 bands with *L. wiegmanni* and *L. occipitalis* in common, as well as an intensely-coloured band no. 3, which is unique for this animal. Furthermore, the bands no. 8 and 9 and especially no. 16 of the animals from the Rio de Janeiro population show very intense colouring due to the application of Coomassie Brilliant Blue. These bands are only faintly visible by the specimens of *L. occipitalis* and *L. wiegmanni*. The results of the morphological examinations, that reveal *L. lutzae* as an easily diagnosable "species", thus can be biochemically-genetically confirmed.

The band spectrum of all three species includes 11 common bands, whereas *L. wiegmanni*'s and *L. lutzae*'s spectrum show 13 bands in common. *L. occipitalis* has no characteristics bands: *L. lutzae* has one, and *L. wiegmanni* even has five.

All the examined blood serum samples were esterase-active, which was to be expected, according to comparable studies done by GORMAN and DESSAUER (1966), WEBSTER, SELANDER and YANG (1972) and WEBSTER and BURNS (1973) with populations of the Iguana-genus *Anolis*.

Under the respective densitograms the distributional pattern of the bands was drawn schematically, and the bands were numbered consecutively according to their speed of migration within the gel from cathode to anode.

For the populations of *L. occipitalis* the results are uniform: maximum activity close to the anode (bands 13/14) and cathode (bands 1/2) and in varying intensity around band 7; in between a few faintly esterase-active bands (6, 9 - 12 and 16) appear. The band variations near 16 seem to be controlled by a polymorphic esterase-locus.

The population of *L. wiegmanni* from Tapes shows a typical picture of esterase activity, though a distinctly different one from that of *L. occipitalis*: the maximum activity (by band 15) corresponds approximately to *L. occipitalis*' bands 13/14, is closer, however, to the anode; bands 1, 2 and 7 are clearly less intense than by *L. occipitalis*; the bands 3, 4 and 5 only appear by *L. wiegmanni*. *L. lutzae* from Rio de Janeiro shows five monomorphic bands. The activity within the range of bands 1 and 2 is even less intense than by *L. wiegmanni*, but bands 7 and 8 are more intensely coloured; the maximum activity here, too, is near band 15.

#### 3.2.4 Ecological-ethological Criteria

The three Brazilian *Liolaemus*-species prefer more or less open sandy areas and are able to bury themselves in the sand. By studying the different populations more closely, one can observe noteworthy particularities characteristic to each species.

*L. occipitalis* has a distinct annual periodicity, though we do not know anything about the seasonal course of its spermiogenesis yet. After a period of dormancy (April to July) the females lay two pure white eggs in October/November. Where and under what moisture-conditions this occurs is unknown (terrarium observations), but most likely not in the dry dune sand. The animals live exclusively on recent dunes undergoing redistribution by the wind. In these dunes they dig their burrows, the entrances to which are often quickly filled with sand. Sometimes the passages lead down as far as the groundwater level. In Jardim do Eden (e.g. September 3rd, 1977) by an air temperature of 16 °C (10 clock) and strong insolation, animals were observed repairing their burrows on low

dune islands that were completely isolated by wide barriers of water. Their burrows went down to about 40 cm deep (8,6 °C) and almost always ended in groundwater. Since the animals' habitat lies within dunes, swamp and lakes and is constantly in danger of being flooded, the question arose, as to whether the animals are able to swim, which seems a strange question to pose about animals living in sand dunes. On September 4th, 1977, an experiment was made using one male from Jardim do Eden and one from Laguna: in the laboratory of the Instituto de Biociências of the Universidade Federal do Rio Grande do Sul, the two animals were put to a "swimming test" in 16 °C-water. Surprisingly it was discovered that the animals can "swim" up to six hours without much difficulty.

On the white sand of the wandering dunes the animals are excellently protected by their mimetic colouring. When disturbed, they chase across the sand, but quickly bury themselves after several meters. A characteristic and distinctly visible curved imprint in the sand, caused by the movements of the tail, betrays the hidden animal lying a few centimeters beneath the surface. Certainly the size of the sand grains is of decisive importance for this fast burying operation. Grain sizes of many dune sands have been determined (e.g. BIGARELLA 1965, BIGARELLA et al. 1966, MARTINS 1967).

For the very uniform sands by Tapes, the locality of *L. wiegmanni*, we found grain sizes between 1 mm (99,99 %) and 2 mm (0,01 %). Sand samples from Tramandai (locality of *L. occipitalis*) corresponded to the grain size distribution indicated by MARTINS (1967):

0,5 mm	= 11,27 %
0,3 mm	= 70,31 %
0,2 mm	= 14,69 %
0,1 mm	= 2,35 %
0,05 mm	= 0,01 %

*L. wiegmanni* avoids the migrating dunes altogether and lives by Tapes on fossil dune sands of much bigger grain size. Fleeing animals do not bury themselves immediately, but try first to reach the closest bush or the protection of *Cereus peruvianus*, from which point they watch their pursuer. Further attempts to catch them cause the animals to bury themselves, but not as completely as *L. occipitalis*: often the end of the tail sticks out of the sand. When the animals dig their burrows in slopes, they always seek the protection of vegetation *wiegmannii* also hibernates (April to July) and the females lay two eggs in October/November.

Like *wiegmannii*, *L. lutzae* does not bury itself immediately when chased, but tries to reach the closest cactus bush (cf. description of the vegetation in DANSEREAU 1947, RIZINI 1976, ULE 1901 etc.) or prickly dwarf palm. At Recreio dos Bandeirantes (Rio de Janeiro) the animals build burrows in the river banks almost 1 m deep. In whose vicinity they live, behaving almost like the European lizard *Lacerta agilis*. At Praia da Tijuca they chase across the open sand, but always stay near prickly dwarf palms. Under the torn-off and wind-drifted remains of *Ipomoea* one often finds several individuals sitting close together. Only when chased persistently do they bury themselves.

Of the three species, *L. occipitalis* is undoubtedly the ecologically best-adapted to the migrating dunes of the Restinga, while *L. lutzae* and *L. wiegmanni* are genuine Restinga-species, i.e. more adapted to the wooded belt along the coast. We would therefore call



*occipitalis* a "sand dune species" and *lutzae* a "Restinga-species" (sensu stricto). *Wiegmannii* was found exclusively on pleistocene or tertiary sands (e.g. western bank of the Lagoa dos Patos) or on sandy river banks. However, the possibility that this species inhabits other biotopes, as well, cannot be excluded, considering its wide range of distribution.

### 3.2.5 Distribution

There are no localities known where sympatry or hybridization occurs. While the distribution of *occipitalis* and *lutzae* is basically clarified, numerous chorological questions about *wiegmannii* remain. Undoubtedly the presumption that this species also occurs in Chile (terra typica), just as the allusion to a patagonian distribution by BURT and BURT (1931) is based on an error. "*L. wiegmannii* ist zweifellos eine nördlichere Form, die Mit-telargentinien bewohnt und bis nach Uruguay vordringt" (HELLMICH 1950, p. 352). LEMA and FABIAN-BEURMANN (1977) report *L. wiegmannii* from the banks of the Laguna Garzón by Rocha (Uruguay). One specimen from the Province of Buenos Aires (SMF 11147, leg. C. Berg) (without further description of the locality) corresponds to the *wiegmannii* specimens from Tapes.

### 3.3 Discussion

Morphological, ethological, electrophoretic, ecological and chorological findings clearly support the assumption that the allopatric *L. wiegmannii*, *lutzae* and *occipitalis* are representatives of a superspecies-complex. Within this complex *wiegmannii* is undoubtedly closest to the ancestral form. Morphologically (e.g. number of scales around the center of the rump, colouring), as well as ethologically (flight behavior), ecologically (Restinga-species) and electrophoretically (esterase-pattern), *wiegmannii* and *lutzae* resemble each other most closely. *Occipitalis*, as a life form of the shifting sand dunes, is confined to the recent dunes. Since *wiegmannii* lives on fossil (pleistocene) dunes exclusively ("The age of the Serra de Tapes laterite and the Itapoa dune fields are probably older Pleistocene or possibly younger Tertiary". DELANEY 1966, p. 24), postglacial phases of dune formation were certainly unable to initiate a northward migration of the populations. A totally different picture prevails for *occipitalis*: the recent area of this taxon can only be explained by an assumption of postglacial dune migration routes (e.g. isolated occurrence at Florianópolis).  $C^{14}$ -data for postglacial deposits with *Anomalocardia brasiliensis* in the coastal plain of Parana (Rio Vermelho) suggest that 5.700 years ago the sea level in this region was 1,5 m higher than at present and that the climate was warmer and more humid (BIGARELLA 1971). The following phase of dune formation certainly had substantial influence on the northern boundary of the *occipitalis* area. BIGARELLA's observation (1971, p. 12) should not be overlooked, however: "No pleistoceno Brasileiro ocorreram várias episódios de expansão e retração dos campos e dunas" (cf. also AB'SABER 1970). Of course the history of the Lagoas, which are closely linked with the sand dunes, must also be considered:

"... it may be inferred that wind generated currents from the North and longshore drift from the South have played important roles in the formation of the coastal plain. The two coastal lakes, Lagoa Mangueira and Lagoa dos Peixes, were formed when longshore drifted sandy materials gradually locked off parts of the sea by recurved spits. Since longshore drift from the south is stronger, the Lagoa Mangueira was completely locked off

from the ocean, whereas the Lagoa dos Peixes intermittantly possesses an outlet. Other smaller lakes in the lower coastal plain were formed by local accumulations of rain and run-off water deprived of effective outlets by large winddrifted sand dunes" (DELANEY 1966, p. 23).

It can currently be supposed that populations similar to *wiegmannii* coming from the South already lived in Uruguay and Rio Grande do Sul during the Wisconsin glacial. The pleistocene conditions ("In front of the continental glaciers from the Province of Entre Rios, Argentina, throughout Uruguay, and in Southern Rio Grande do Sul loess pampas existed. North of the loess pampas and south of the Serra Geral escarpment a cold steppe was probably present" (DELANEY 1963, p. 52; as to climate cf. AB'SABER 1970, ANDRADE et al. 1963, FRÄNZLE 1976, HURT 1964, MERCER 1976, MÜLLER 1973, 1975, STEVENSON and CHENG 1969, VAN DER HAMMEN 1974) and the height of sea level at the end of the Wisconsin, then 50 m below its present. Height, constitute the main external reasons for a northward migration of *Liolaemus* populations as far as

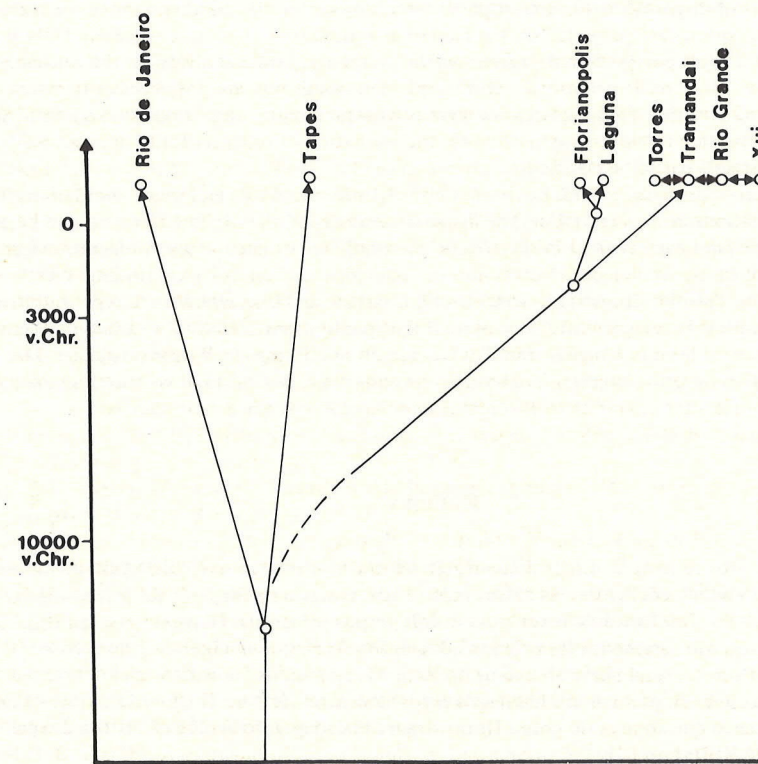


Fig. 2:  
Evolution of the *Liolaemus wiegmannii*-Complex (after MÜLLER and STEINIGER 1977).

Rio de Janeiro. Due to the postglacial rise in sea level this possibility is eliminated and phases of dune formation are only of importance to the ecological dune specialist, *L.*



*occipitalis*. While the phylogenetic separation between *lutzae* and *wiegmannii* can be understood first of all as the disjunction of originally uniform populations, for *occipitalis* the immigration of pre-adapted ancestors into a habitat with special selective conditions has to be assumed. The means, however, that we can only roughly determine the point in time of this immigration and hence the rate of evolution of this species.

### Summary

An analysis of the dispersal centres of terrestrial vertebrates in the Neotropical realm revealed that at last 40 centers exist. A study of the relationships between the individual centres, based on the phylogeny of their faunal elements resulted in the classification of the centres into three main groups. The faunal elements of Group I (non-forest) are characterized by their adaption to unforested or at least partially-unforest biomes, generally below 1500 m. The faunal elements do not occur in the rain forest biomes, which are inhabited by the elements of Group II (forest and montane forest), while those of Group III show an ecologically restrict adaption to the treeless high-mountain region (oreal).

The analysis of dispersal centres presupposes three steps. First the minimum ranges of species, semispecies and subspecies are projected on the map of a continent or an animal kingdom. Only in rare cases do individual ranges possess common areas on the periphery, however always in the nuclear area where they overlap. That the distributional centres obtained in this way are not necessarily centres of origin, was numerous studies. These centres are regions with maximum range diversity. In a third step, which is usually forgotten in biogeographical work, the formation of subspecifically or semispecifically differentiated vicariants has to be clarified.

The position of dispersal centres has been decisively influenced by Quaternary oscillations in climate and fluctuations in the vegetation. The dispersal centres and their faunal elements can be used to indicate how the landscape evolved in the area in question. One example is the *Liolaemus wiegmanni* Complex. Morphological, ethological, electrophoretic, ecological and chorological findings clearly support the assumption that the allopatric *L. wiegmanni*, *L. lutzae* and *L. occipitalis* are representatives of a superspecies-complex. It can currently be supposed that populations similar to *wiegmannii* coming from the South already lived in Uruguay and Rio Grande do Sul during the Wisconsin glacial. The pleistocene conditions and the height of sea level at the end of the Wisconsin, constitute the main external reasons for a northward migration of *Liolaemus* populations as far as Rio de Janeiro.

### Resumo

Uma análise dos centros de dispersão da região neotropical revelou que existe pelo menos 40 centros. Um estudo de relações entre os centros individuais, baseado na filogenia de seus elementos faunísticos resultou na classificação dos centros em três grupos principais. Os elementos faunísticos do grupo I (não floresta) são caracterizados pela sua adaptação ao campo ou a biomas pelo menos parcialmente sem floresta, geralmente abaixo de 1500 m. Os elementos faunísticos não ocorrem nos biomas de floresta churosa, os quais são habitados pelos elementos do grupo II (floresta e floresta de montanhas), enquanto que aqueles do grupo III mostram uma adaptação ecológica restrita à região de campo de montanhas altas (oreal).

A análise de centros de dispersão é feita em 3 etapas. Na primeira são projetados os territórios mínimos de espécies, semiespécies e superespécies em uma mapa de um continente ou de um reino animal. Somente em casos raros os territórios tem periferia em comum no entanto a superposição das periferias, forma o centro do Território. Que os centros de distribuição obtidos desta maneira não são necessariamente os centros de origem, já foi objeto de muitos estudos. Esses centros são regiões com a máxima diversidade de territórios. A terceira etapa que geralmente é esquecida nos trabalhos biogeográficos, se ocupa com o esclarecimento da formação de vicariantes diferenciados subespecificamente or semi-especificamente.

A posição dos centros de dispersão foi influenciada decisivamente por oscilações climáticas e da vegetação do quaternário. Os centros de dispersão e seus elementos faunísticos podem ser usados como indicadores da evolução da área em questão. Um exemplo é o complexo do *Liolaemus wiegmanni*. Estudos morfológicos, etológicos, eletroforéticos, ecológicos e corológicos apoiam a suposição de que os alopátricos *L. wiegmanni*, *L. lutzae* e *L. occipitalis* são representantes de um complexo de superespécies. Pode-se supor que populações semelhantes a *wiegmannii* vindo do sul, viveram no Uruguai e no Rio Grande do Sul durante a glaciação de Wisconsin. As condições pleistocénicas e o alto nível do mar no fim da glaciação de Wisconsin, são as principais causas externas para a migração em direção ao norte de populações de *Liolaemus* para o Rio de Janeiro.

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Author's adress:

Prof. Dr. rer. nat. Paul Müller  
Universität des Saarlandes  
Lehrstuhl für Biogeographie  
6600 Saarbrücken  
BR Deutschland

Accepted for publication in Juni 1978